Statocysts in Crabs: Short-Term Control of Locomotion and Long-Term Monitoring of Hydrostatic Pressure

PETER J. FRASER

Zoology Department, Aberdeen University, Tillydrone Avenue, Aberdeen AB24 2TZ Scotland

Abstract. Crabs show well-coordinated locomotion. They have proprioceptors similar to those of lobsters, but they differ in terms of their balancing systems and their condensed nervous system, which allows rapid interganglionic conduction. Typically they exhibit dynamically stable locomotion with a highly developed semicircular canal system that codes angular acceleration in each of three orthogonal planes (horizontal and vertical at 45° and 135° to the pitching plane). Left and right interneurons each code one direction of angular acceleration, carrying information between the brain and the thoracic ganglia. Cell A codes head-up vertical plane angular accelerations. Cell B codes rotations in the horizontal plane. Interneurons C and D code head-down vertical plane information, carrying it ipsilaterally and contralaterally respectively. These interneurons have a central role in locomotion. They are activated and have their responsiveness to angular acceleration enhanced before and during locomotion. Such simple activation pathways point to how an angular-acceleration-controlled robot (CRABOT) could be constructed. Hydrostatic pressure information carried by the thread hairs, which also sense angular acceleration, is filtered out from direct pathways onto the interneurons, but spectral analysis shows that it still has an influence *via* central pathways. Long-term recordings from equilibrium interneurons in free-walking crabs taken from the wild into constant conditions show tidally changing frequencies of bouts of activity, with peaks that correspond to times of high tide.

Introduction

Brachyuran crabs are conspicuous animals that occupy a variety of habitats and show well-coordinated locomotor ability while walking, crawling, climbing, swimming, or burrowing under a variety of hydrostatic pressure conditions. Compared with the ladder-like nerve cord of macrurans (crayfish and lobsters), their nervous system shows condensation and fusion of thoracic ganglia, allowing rapid interganglionic conduction of impulses. The abdomen has been much reduced and, in contrast to that of macrurans, is little used in normal or escape swimming. These crabs can survive leg autotomy: 13%–43% of individual *Carcinus* sampled from the wild have missing legs (McVean, 1982). Typically they exhibit dynamically stable locomotion, with statocyst (or balancing organ) interneurons having a central role (Fig. 1; Fraser, 1982; Fraser *et al.*, 1987). Thread hair receptors, which respond to fluid displacements in the statocyst, have been shown to have their spontaneous activity and sensitivity to angular acceleration modulated by small changes in hydrostatic pressure (Fraser and Macdonald, 1994; Macdonald and Fraser, 1999). Clearly, elucidating the simplifying principles underlying such versatility and diversification of function is an important aim. One approach to dissecting such complexity is to concentrate on a fundamental difference between crabs and lobsters—that is, the elaboration in crabs of the statocyst and its central pathways.

Statocysts and Leg Proprioceptors Involved in Locomotion

The statocyst contains a statolith and angular acceleration receptors. In the crab, the crescent of statolith hairs (Sand-

Brain

C

Thread Hairs

A

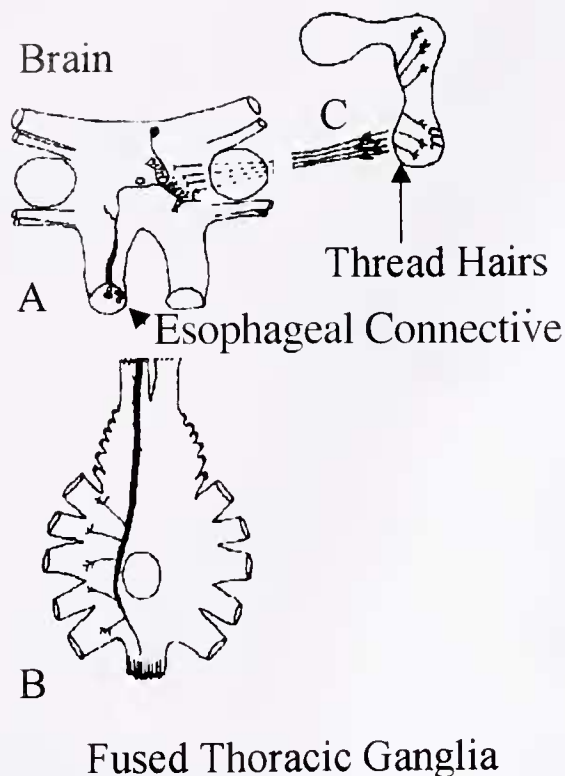**Esophageal Connective**

B

Fused Thoracic Ganglia

Figure 1. Equilibrium cell A in brain (A) and thoracic ganglia (B) of the crab *Carcinus maenas*. The large axon runs in the esophageal connective. Thread hair afferents (C), which are activated by angular acceleration in the plane of the vertical canal of the statocyst, contact the equilibrium interneurons directly. (Redrawn from Fraser, 1989).

eman and Okajima, 1972) is much smaller than the macruran crescent (see Lemmnitz and Wolff, 1990). The fluid-filled sac has been shaped from a simple cavity in the macruran statocyst into two orthogonal semicircular canals. Angular accelerations in the planes of the horizontal or vertical canals are monitored by a row of long, slender thread hairs (Fig. 1C; Sandeman and Okajima, 1972; Fraser and Takahata, 2001). Typically the response of thread hairs to an angular acceleration is unidirectional, with two oppositely responding directional classes. Analogous to those of vertebrates, the receptors integrate angular acceleration and code angular velocity in the horizontal plane or in vertical planes either at 45° or at 135° to the median line. Thread hairs are the main sensory component involved in a variety of statocyst-driven behaviors ranging from walking to eyestalk movement, with free hook hairs and statolith hairs playing a lesser role (Cohen and Dijkgraaf, 1961; Fraser, 1989; Fraser and Takahata, 2001). An inertial angular acceleration detector based on an orthogonal semicircular canal system could be easily added to a robot by using connectivity and coding principles derived from crab equilibrium interneurons, which are described below.

Crabs normally walk sideways. The leading legs pull and

the trailing legs push to move the body (Clarac and Coulmance, 1971; Evoy and Ayers, 1982). Crabs do not exhibit regular gait patterns, but have a great variety of gaits and leg activation sequences. Hence Evoy and Ayers (1982) state that "changes in gait occur and conditions strictly satisfying the alternating tetrapod gait are rarely seen." During high-speed running, ghost crabs may even become bipedal, with only two legs alternating on the trailing side (Burrows and Hoyle, 1973). Statocyst ablation affects sideways walking and the rearing reflex (Cohen and Dijkgraaf, 1961; Fraser, 1974). Swimming activity is more stereotyped and again highly dependent on statocyst input (Fraser *et al.*, 1987). During swimming, all muscles in the fifth legs are active in a sequence that causes cyclical sculling. Only muscles that operate joints controlling dorsolateral movements are involved in sideways walking, and they are used in a different temporal pattern than in swimming (Fraser *et al.*, 1987).

Leg proprioceptors are used in the fine motor control to produce coordinated behavior, but during rhythmic behavior, sensory information does not vary much on each cycle unless a leg hits an obstacle. A variety of receptors include muscle receptor organs, which measure muscle stretch (Bush, 1977); chordotonal organs, which are articular (joint rotation) receptors measuring stretch around joints; and apodeme receptors and cuticular stress receptors, which record muscular tension *via* tendons and cuticle respectively (Wales *et al.*, 1971). The funnel canal organs at the ends of the dactylopodites must be silent for the animal to swim, whereas their rhythmic firing in walking is used for step regulation (Libersat *et al.*, 1987). Although it is not possible here to do justice to the complexity of information relayed by these proprioceptors, in general their role in locomotion in crabs is broadly similar to that in lobsters and crayfish.

Equilibrium Interneurons Involved in Locomotion

The angular acceleration sensors, the thread hairs, project onto a small set of eight large interneurons that link the brain to the fused thoracic and abdominal ganglia (Fig. 1; Fraser, 1974, 1990). These fire in the short term during angular accelerations caused by locomotion (Fig. 2A, B; Fraser, 1982), but are also activated centrally before and during bouts of walking or swimming (Fig. 2B; Fraser *et al.*, 1987; Fraser, 1975, 1989). Their activity long term consists of quiescent periods with short bouts of extremely elevated activity. Cells are not coupled and are more likely to act in anti-phase during short-term oscillations that form part of the locomotion. Over a longer time scale, on the order of minutes, their overall activity is well synchronized. Vector information is hence preserved (Fraser *et al.*, 1997, 2001). During these bouts of firing, the gain in the statocyst pathways alters greatly so that perturbations of angular acceleration have a large effect (Fig. 3).

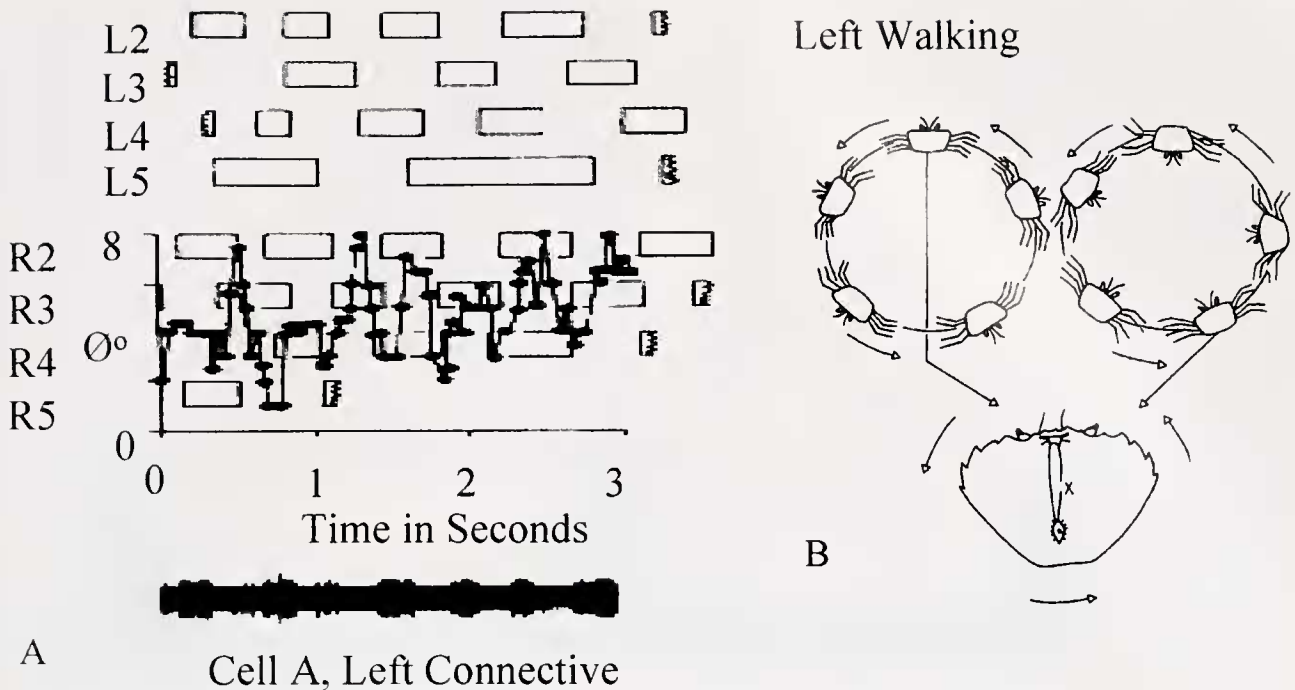In the context of discussing the role of the interneurons in

Figure 2. (A) Extension phases of left and right 2nd to 5th legs during a short sequence of walking to the left by a crab. The extracellular recording shows cell A in the left esophageal connective. The series of bursts of activity are more related to slight angular excursions of the body (ϕ) than to the gait pattern. ϕ is the clockwise angular displacement of the body of the crab around the horizontal longitudinal axis. (B) The effect of cutting the right esophageal connective on locomotion in the crab *Carcinus maenas*. Gait alters and the crab prefers walking left. Regardless of the direction of walking, the crab always turns counterclockwise (Bethe, 1897). This is the direction that optimally excites Cell B in the right connective. Electrical stimulation of the cut end of the connective will straighten or reverse the counterclockwise movement.

locomotion, Fraser (1982) points out that "where a behavior involves vectorial output in more than one dimension, or where feedback loops are involved, then the output measured by displacement of appendages or by muscle activity is no longer an adequate measure of the behavior . . . in terms of understanding the underlying neural activity, locomotion in crabs may be better described in terms of components of force and torque in the planes used by the equilibrium cells rather than in terms of the gaits employed." The angular displacements of crabs have been monitored in orthogonal planes with a miniature triaxial accelerometer.

Although proprioceptor input affects the activity of the interneurons, their outputs in free-walking animals are not particularly complicated (Fraser, unpubl. data; Fraser, 1995). Interestingly, Cruse *et al.* (1998) and Schmitz (2001) state that in the stick insect there is little evidence for a central pattern generator. Instead sensory information derived from leg position and ground contact, together with six different coupling mechanisms, allows selection between swing networks and stance networks. Lobster walking has been successfully modeled with five main classes of components: central pattern generators, command systems, coordinating systems, proprioceptive and exteroceptive sen-

sors, and phase- and amplitude-modulating sensory feedback (Ayers *et al.*, 1998). Stepping rates for such models are low. It may be that the crab has more similarities to the stick insect model than to the lobster model in terms of its reliance on sensory control, and an orthogonal command set based on the equilibrium interneurons may be sufficient to control a large part of its locomotion.

The finding that the statocyst thread hair receptors alter their activity under the influence of hydrostatic pressure makes understanding of their role more complicated (Fraser and Macdonald, 1994; Fraser *et al.*, 1996; Macdonald and Fraser, 1999). Positive-going and negative-going modulation of thread hair spike frequency is thought to arise from activation of the two directional classes of mechanoreceptors *via* the linking chorda because of the slight volume changes associated with differential compressibility of the cuticle and other tissue components. Although thread hairs respond directly to alterations in hydrostatic pressure, thread hair interneurons do not seem to do so. Tidal period rhythms of firing pattern in equilibrium interneurons occur and match those found for general locomotor activity (Naylor and Atkinson, 1972; Fraser and Takahata, 2001). These are affected by hydrostatic pressure pulses or cycles, and spectral analyses of long sequences show that some of the
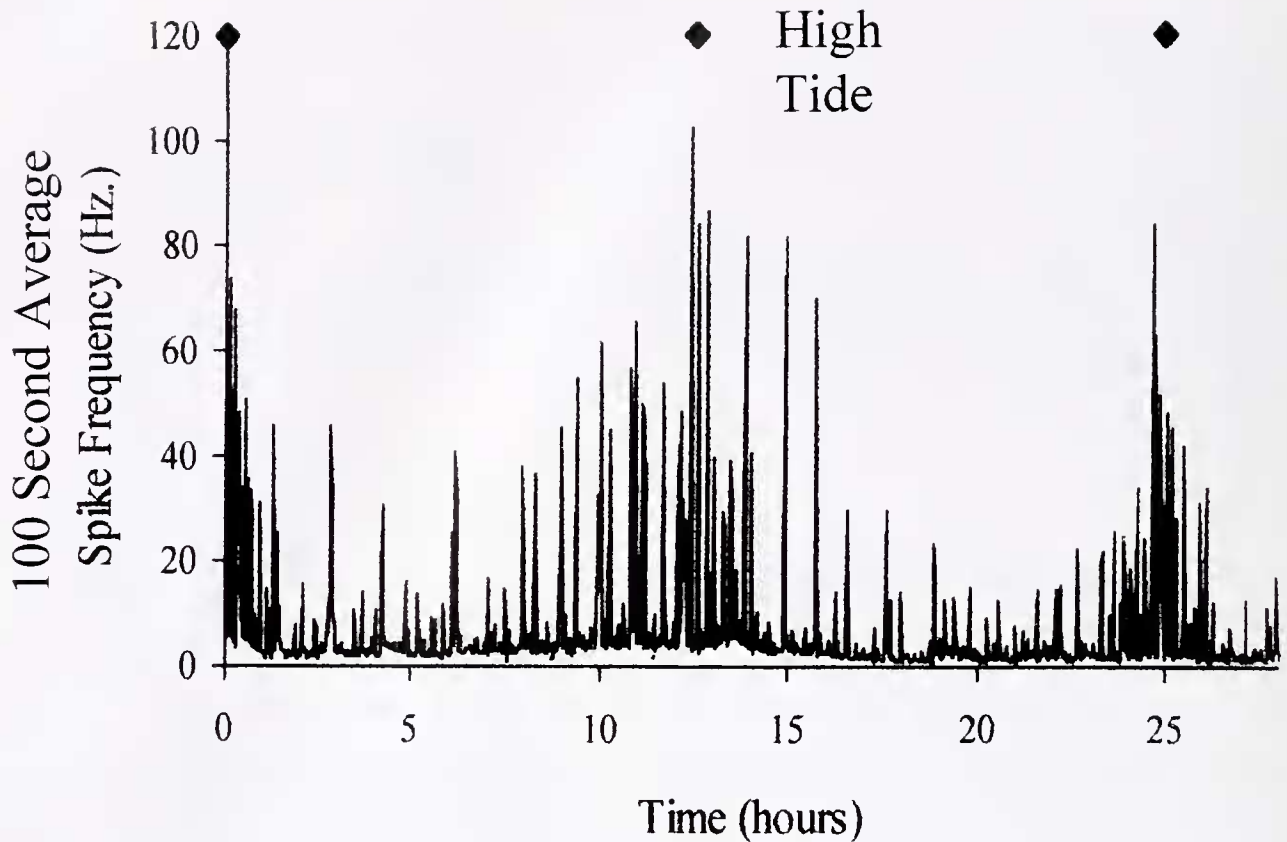
Figure 3. Long-term recording from equilibrium interneurons (spike frequency measured every 100 s) in a free-walking crab, *Carcinus maenas,* taken into constant conditions in an aquarium after capture at low tide. The recording starts 6 h after capture. Arrows mark the occurrence of high tides. High bouts of activity in the cells correspond to locomotor behavior in the crab, and there is clear tidal rhythmicity. (Redrawn from Fraser and Takahata, 2001).

pressure information is getting through, presumably *via* higher order inputs (Fraser *et al.,* 2001).

CRABOTS in the Future

Crabs show well-coordinated but highly variable walking patterns and easy transitions between walking and swimming. Activation patterns of equilibrium interneurons during such movement are simple and should be easily copied. This points the way to how an angular acceleration controlled walking robot (CRABOT) could be constructed, which would advance maneuverability of such robots and should save energy. Optimism for the success of this approach comes from early experiments showing circling movements in crabs when one esophageal connective was cut and reversal of this circling behavior with stimulation of the cut connective. This circling may be explained in terms of the effects on equilibrium cells (Fig. 2B; Bethe, 1897; Fraser, 1982). At present, a major limitation regarding realistic robotic modeling is the stepping frequency of artificial limbs and activators.

Literature Cited

Ayers, J., P. Zavracky, N. McGruer, D. P. Massa, W. S. Vorus, R. Mukherjee, and S. Currie. 1998. A modular behavioral-based architecture for biomimetic autonomous underwater robots. Pp. 15–21 in *Proceedings of the Autonomous Vehicles in Mine Countermeasures Symposium,* 5–9 April 1998. Naval Postgraduate School, Monterey, CA.

Bethe, A. 1897. Das Nervensystem von *Carcinus maenas.* Ein anatomisch-physiologischer Versuch. I. Theil, II. Mittheil. *Arch. Mikrosk. Anat. Entwicklungsmech.* **50:** 589–639.

Burrows, M., and G. Hoyle. 1973. The mechanism of rapid running in the ghost crab, *Ocypode ceratothalma. J. Exp. Biol.* **58:** 327–349.

Bush, B. M. H. 1977. Non-impulsive afferent coding and stretch reflexes in crabs. Pp. 439–460 in *Identified Neurons and Behavior of Arthropods,* G. Hoyle, ed. Plenum Press, New York.

Clarac, F., and M. Coulmance. 1971. La marche lateral du crabe (*Carcinus*): Coordination des movements articulaires et regulation proprioceptive. *Z. Vgl. Physiol.* **73:** 408–438.

Cohen, M. J., and S. Dijkgraaf. 1961. Pp. 65–108 in *The Physiology of Crustacea, Vol. II,* T. H. Waterman, ed. Academic Press, New York.

Cruse, H., T. Kindermann, M. Schumm, J. Dean, and J. Schmitz. 1998. Walknet—a biologically inspired network to control six-legged walking. *Neural Networks* **11:** 1435–1447.

Evoy, W. H., and J. Ayers. 1982. Locomotion and control of limb

movements. Pp. 61–105 in *The Biology of Crustacea, Vol. 4: Neural Integration and Behavior*, D. C. Sandeman and H. L. Atwood, eds. Academic Press, New York.

Fraser, P. J. 1974. Interneurons in crab connectives (*Carcinus maenas* (L.)): directional statocyst fibres. *J. Exp. Biol.* **61:** 615–628.

Fraser, P. J. 1975. Three classes of input to a semicircular canal interneuron in the crab, *Scylla serrata* and a possible output. *J. Comp. Physiol.* **104:** 261–271.

Fraser, P. J. 1978. Vector coding and command fibres. In *The Command Neuron Concept*, I. Kupfermann and K. R. Weiss, eds. *Behav. Brain Sci.* **1:** 3–39.

Fraser, P. J. 1982. Views on the nervous control of complex behavior. Pp. 293–319 in *The Biology of Crustacea, Vol. 4: Neural Integration and Behavior*, D. C. Sandeman and H. L. Atwood, eds. Academic Press, New York.

Fraser, P. J. 1989. Vector coding and multiplicative gain control in the nervous system of the crab. Pp. 95–102 in *New Developments in Neural Computing*, J. G. Taylor and C. L. T. Mannion, eds. Adam Hiliger, New York.

Fraser, P. J. 1990. Equilibrium control by statocyst activated interneurons. Pp. 187–192 in *Frontiers in Crustacean Neurobiology*, K. Wiese, W. D. Krenz, J. Tautz, H. Reichert, and B. Mulloney, eds. Birkhäuser Verlag, Basel.

Fraser, P. J., and A. G. Macdonald. 1994. Crab hydrostatic pressure sensors. *Nature* **371:** 383–384.

Fraser, P. J., and M. Takahata. 2001. Statocysts and statocyst control of motor pathways in crayfish and crabs. In *The Crustacean Nervous System*, K. Wiese et al., eds. Springer Verlag, Berlin. (In press).

Fraser, P. J., M. Bevengut, and F. Clarac. 1987. Swimming patterns and the activity of identified equilibrium interneurons in the shore crab, *Carcinus maenas*. *J. Exp. Biol.* **130:** 305–330.

Fraser, P. J., A. G. Macdonald, and R. N. Gibson. 1996. Low pressure hydrostatic pressure receptors in the crab *Carcinus maenas* (L.). In *Basic and Applied High Pressure Biology IV*. J. C. Rostain, A. G. Macdonald, and R. E. Marquis, eds. *Medsubhyp. Int.* **5:** 59–68.

Fraser, P. J., A. G. Macdonald, S. F. Cruickshank, and M. P. Schraner. 1997. Integration of hydrostatic pressure information by identified interneurons in the crab *Carcinus maenas* (L.); long term recordings. *Proc. R. Inst. Navigation RIN* **97:** 25.1–25.10.

Fraser, P. J., A. G. Macdonald, S. F. Cruickshank, and M. P. Schraner. 2001. Integration of hydrostatic pressure information by identified interneurons in the crab *Carcinus maenas* (L.); long term recordings. *J. Navigation* (In press).

Lemmnitz, G., and H. G. Wolff. 1990. Recording from sensory cells in the statocyst of *Astacus*. Pp. 97–105 in *Frontiers in Crustacean Neurobiology*, K. Wiese, W. D. Krenz, J. Tautz, H. Reichert, and B. Mulloney, eds. Birkhäuser Verlag, Basel.

Libersat, F., F. Clarac, and S. Zill. 1987. Force sensitive mechanoreceptors of the dactyl of the crab: single unit responses during walking and evaluation of function. *J. Neurophysiol.* **57:** 1618–1637.

Macdonald, A. C., and P. J. Fraser. 1999. The transduction of very small hydrostatic pressures. *Comp. Biochem. Physiol. A* **122:** 13–36.

McVean, A. 1982. Autotomy. Pp. 107–132 in *The Biology of Crustacea, Vol. 4: Neural Integration and Behavior*, D. C. Sandeman and H. L. Atwood, eds. Academic Press, New York.

Naylor, E., and R. J. W. Atkinson. 1972. Pressure and rhythmic behavior of inshore marine animals. *Symp. Soc. Exp. Biol.* **26:** 395–416.

Sandman, D. C., and A. Okajima. 1972. Statocyst-induced eye movements in the crab *Scylla serrata I*. The sensory input from the statocyst. *J. Exp. Biol.* **57:** 187–204.

Schmitz, J., J. Dean, T. Kinderman, M. Schumm, and H. Cruse. 2001. A biologically inspired controller for hexapod walking: simple solutions by exploiting physical properties. *Biol. Bull.* **200:** 195–200.

Wales, W., F. Clarac, and M. S. Laverack. 1971. Stress detection at the autotomy plane in the decapod crustacea. 1. Comparative anatomy of the receptors of the basi-ischiopodite region. *Z. Vgl. Physiol.* **73:** 357–382.